THE DEVELOPMENT AND COMPARATIVE STRUCTURE OF THE GIZZARD IN THE ODONATA ZYGOPTERA.

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The following study[1] was undertaken on the advice and under the direction of Dr. Philip P. Calvert, instructor in Zoölogy in the University of Pennsylvania.

Dr. Ris' work on the gizzard of the *Odonata* and Dr. Calvert's study of Californian forms strongly suggested the phylogenetic importance of this organ.

The present study has been limited to the more primitive *Odonata*—the suborder *Zygoptera*.

I am indebted to Dr. Calvert for the material placed at my disposal, for many of my preparations, including his slides used in his paper of 1899 mentioned later, for the determination of genus and species in every case, and for the suggestion of the structural formula used in describing the gizzards.

In 1896, Dr. F. Ris published[2] a paper entitled *Untersuchungen über die Gestalt des Kaumagens bei den Libellen und ihren Larven.* The results of his investigations are briefly outlined here:

In the *Odonata* the fore-gut extends to the third abdominal segment. In larva and imago alike the gizzard is found at the posterior end of the fore-gut in the second abdominal segment. It is formed by a thickening of the muscle layer, and by a modification of the chitinous coat of the fore-gut to form folds armed with teeth. The number of these folds is four, eight or sixteen. The metamorphosis to the imago shows a regular reduction in the strength and complication of the elements, but their number varies greatly. At the metamorphosis, the larval lining is shed with the chitinous coat of the exterior of the body; Dr. Ris states that he found in a *Libellula*, directly after metamorphosis, the old gizzard lining enclosed within the new. He examined the larval and adult

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[2] *Zoolog. Jahrbüch.*, IX.

form of *Calopteryx virgo*, *C. splendens*, *Pyrrhosoma minium*, *P. tenellum*, *Agrion puella* and *pulchellum*, *Erythromma* (*najas*), *Enallagma* (*cyathigerum*), *Ischnura* (*elegans*) and *Platycnemis pennipes*, *Lestes virens*, *Gomphus*, *Æschna*, *Anax*, *Cordulegaster annulatus* and *bidentatus*, *Cordulia ænea*, *Diplax*, *Libellula*, *Orthetrum*.

The conclusions drawn by Dr. Ris from his investigations are as follows:

Larvæ.—The original form of the gizzard shows a division into sixteen longitudinal folds, eight broad and eight narrow, which bear an armature of irregularly placed teeth. This type is found in the *Calopteryginæ*.

A higher development of the organ appears in the typical group of the *Agrioninæ*; the sixteen folds show a greater number of teeth and a more complicated arrangement of these.

The legion *Lestes* shows a reduction of the sixteen folds to eight, apparently through the loss of the smaller folds. These eight folds are again divided into four broad and four narrower folds. In the *Anisoptera* (*Gomphus* and *Æschna*) there is reduction to four equal, similar folds. Finally, *Cordulegaster* and the *Libellulidæ* differentiate the folds into two pairs of teeth, so that the original radial symmetry is changed to bilateral.

Imagos.—The series easily traced in the larval forms is somewhat confused in the imagos, owing to the reduction which invariably occurs. The least reduction from larva to adult is found in the *Calopteryginæ*; more is shown in the *Agrioninæ*, where is seen the tendency to eliminate the smaller fold in certain individuals; the strongest reduction occurs in *Gomphus* and *Æschna*; in *Cordulegaster* and in the *Libellulidæ* scarcely more than a hint of the relation to the larva remains.

This purely morphological development from the radial symmetry of numerous elements of an organ to the bilateral symmetry of a few elements runs parallel with the phylogenetic relationships of the single groups.

In a paper on the *Odonata* from Tepic, Mex.,[3] 1899, Dr. Calvert gives notes on the gizzards of the forms studied by him. Contrary to Dr. Ris and other previous writers, he finds the position of the junction of fore- and mid-gut, and therefore of the

[3] *Proc. Cal. Acad. of Sciences* (Third Series, Vol. I, No. 12, 1899).

gizzard, to be very variable. He examined the gizzards of *Hetærina americana*, *Archilestes grandis*, *Lestes tenuatus*, *Argia pulla* and *agrioides*, *Erythagrion salvum*, *Ischnura Ramburii* var. *credula*, *Anax junius*, *Herpetogomphus elaps*, *Pantala hymenæa*, *Pseudoleon superbus*, *Tramea onusta*, *Dythemis sterilis*, *Micrathyria Hageni*, *Orthemis ferruginea* and *Diplax corrupta*.

Dr. Ris and Dr. Calvert agree generally on the morphology of the forms studied by both. They differ, however, in the phylogenetic position of the legion *Lestes*.

Dr. Calvert does not draw any phylogenetic conclusions from his studies, considering the examination of many more forms necessary before this can safely be done.

Preparation of Present Material.—The present study has been based upon representatives of the sub-families *Calopteryginæ* and *Agrioninæ* collected from every continent.

The preparations have largely been made from dried[4] specimens. From these the abdomens were cut off at the base of the third segment and soaked in seventy per cent. alcohol until softened. Some of these, even after long soaking, were so brittle that only fragments of the gizzard could be mounted. In cases where, because of its fragmentary condition, the structure of the gizzard is at all doubtful, I have put an interrogation point after the descriptive formula. The remainder of the material studied had been preserved in alcohol or formaline.

To obtain and prepare the chitinous lining of the gizzard for study, the abdomen was slit open along one of the membranous pleura, the gizzard located, and separated from the rest of the alimentary canal by a fine pair of scissors. The gizzard was cut open, the muscular coat removed with needles, and the chitinous lining spread out flat upon a slide. After cleaning, this was mounted in Canada balsam, making a very distinct preparation for study. In nearly every case the dried specimens from which the gizzards have been removed have been again put together, so that their value as ordinary museum material has been little, if at all, impaired.

The larvæ studied belong mainly to the sub-family *Agrioninæ*. They were collected from the vicinity of Philadelphia and were either fresh or preserved in alcohol.

[4] See the report of the meeting of the Academy of Natural Sciences of Philadelphia of January 17, 1899, in *Science*, Vol. IX, p. 183.

Development of the Gizzard.

The gizzard is a specially thickened and cuticularized portion of the alimentary canal, appearing at the junction of fore- and mid-gut, and projecting slightly into the latter. Externally is a coat of circular muscle fibres, thicker in the larvæ than in the adult and varying in thickness in adults of different genera. Within is a layer of epithelial cells, at first one cell in thickness, but later becoming many cells thick in definite areas, to form folds projecting into the lumen of the canal.

In the forms examined, four folds or some multiple of four to as many as thirty-two have been found—sixteen and eight being the numbers most commonly occurring.

From the epithelial cells is developed the inner chitinous coat of the gizzard, which is thin on the spaces between folds, becoming thickened on the folds and forming here horny teeth of various sizes.

The writer has examined Agrionine larvæ from the time of hatching to the period immediately preceding metamorphosis.

In larvæ just hatched no evidence of any gizzard-armature was found.

The following statements refer to larvæ of *Ischnura verticalis* Say:

In larvæ 3 and 4 mm. in length[5] the gizzard is quite clearly marked (fig. 25). The chitinous coat shows sixteen folds or fields, eight larger alternating with eight smaller. Each larger field is armed with teeth arranged in two groups, an anterior and a posterior, the latter occupying about the centre of the gizzard. The posterior group consists of two large pointed teeth, each enclosed on its outer side by four to five small teeth. The anterior group comprises two pointed narrow teeth intermediate in size between the two sets mentioned above.

Each smaller field has one group of three to four small teeth, which are at the same level as that of the posterior group of the larger fields.

A larva 6 mm. long shows practically the same armature, but on the smaller fields also there are often two groups, the anterior comprising one to two teeth, the posterior three to four.

[5] In all of these larvæ, by length I mean the distance measured from the external anterior part of the head to the posterior limit of the last abdominal segment, the gills being excluded.

A larva 8 mm. long shows considerable difference in the size and number of the teeth (Pl. IV, fig. 26). The anterior groups of both fields show an increase in the number of teeth, which remain approximately the same in size. In the posterior groups the smaller teeth show decrease in size with increase in number; the two large teeth of the larger fold remaining the same in size.

A larva of 10 mm. length shows much the same structure.

Three larvæ of 15 mm. length show the same line of development carried a little further (fig. 27), an increase in number of the teeth of the anterior groups of both folds, slight increase in number with continued decrease in size of the small teeth of the posterior groups of both folds.

In all larvæ studied the gizzard was found in the second abdominal segment.

Young imagos of *Ischnura verticalis* were examined soon after metamorphosis. In those dissected directly after the spreading of the wings only the larval gizzard was observed. This lay in the sixth segment. In an adult in which the coloring was distinctly developed, the larval gizzard lining lay immediately within that of the adult, which latter bore a very different armature (Pl. III, fig. 17). In still other individuals the adult gizzard was in the sixth segment, while the lining of the larval gizzard and of the fore-gut of the larva, coiled up in a mass, lay in the lumen of the canal in the seventh segment. These observations suggest the possibility of learning something of the structure of the gizzard of the larvæ of *exotic* species by inspecting the contents of the alimentary canal of imagos whose colors show them to have but recently transformed.

To sum up the development of the gizzard lining in *Ischnura verticalis*, it is seen that from its earliest appearance (which in the present study was found in a larva 3 mm. long) there is a steady increase in the number of teeth on all folds with a decrease in size in those of posterior groups. At metamorphosis the gizzard moves backward from the second to the sixth abdominal segment. A new chitinous coat is formed on the fore-gut, with a new gizzard armature. The larval lining lying within the adult lining becomes loosened from it and finally separates entirely, and is found, within a few hours after metamorphosis, lying coiled up within the canal. It is probable that in still older imagos the cast-off larval gizzard lining lies still further posterior in the canal, and is finally voided through the anus.

The Gizzard of Various Adults.

The position of the gizzard in the imago was found to vary from the third abdominal segment to the seventh. In the majority of forms examined the gizzard lies in the centre or posterior extremity of the sixth segment; in a small number it lies in the fifth, in a still smaller in the seventh, and in a very few in the third or fourth segment.

Variations in the position are frequently found in different species of the same genus and even in different individuals of the same species.

A male of *Calopteryx apicalis* had the gizzard in the anterior end of the sixth segment, a female in the centre of the fifth; while in a male of *C. cornelia* it was located in the fifth segment.

In a male of *Phaon iridipennis* the gizzard was found in the posterior end of the sixth segment; in a male of *P. fuliginosus* in the third, and in a female of the same species in the sixth segment.

In four species of *Vestalis* the position varied only from the posterior end of the fifth to the middle of the sixth segment. The same variation was seen in five species of *Hetærina*, and likewise in four species of *Euphæa*.

In the ♀ of *Libellago caligata* the gizzard was found in the third segment, in tne ♂ in the fifth, and in *L. curta*, ♂, in the fourth segment. In four individuals—two species—of *Micromerus* it was found in the fifth; in *Thore boliviana*, ♂, in the centre of the fifth, in ♀ in anterior end of seventh; in *Euthore hyalina*, ♂, in the anterior end of sixth, in ♀ in posterior end of fifth.

Of the *Agrioninæ*. legion *Pseudostigma*, its position varied in eight individuals, of five genera, from the middle of the sixth to the anterior extremity of the seventh segment; in the Legion *Podagrion*, in five males and one female of *Paraphlebia* sp. (group of *Zoe*), the position varied only from the anterior end to the centre of the sixth segment; in five species of the genus *Heteragrion*, from the posterior end of the fifth to the anterior of the seventh; in the legion *Platycnemis*, in four genera, the organ was found in the sixth or seventh segment; in the legion *Protoneura*

—in three species of *Disparoneura*, in three of *Neoneura* and in three of *Protoneura*—the same variation is seen, from the posterior end of the sixth to the anterior of the seventh; of the Legion *Agrion* it appears in the sixth segment in *Hyponeura lugens*, *Ischnura heterosticta*, *Enallagma ebrium*, *geminatum* and *aspersum*, in *Nehalennia lais*, *Ceriagrion glabrum*, *Anisagrion allopterum* and *Hemiphlebia mirabilis;* in the fifth in *Argia putrida*, *Pyrrhosoma tenellum;* in the seventh in *Leptagrion macrurum* and *Leptobasis vacillans;* of the legion *Lestes* it appears in the sixth segment in *Lestes disjuncta* and *L. leda.*

Armature of the Adult Gizzard.

To save the necessity of giving lengthy descriptions of the armature of each gizzard studied, and more especially to render the comparison of these armatures more easy, it was found convenient to construct a formula whereby the general structure of the armature might be indicated.

Below is given an explanation of the formulæ used:

F, F, f, indicate specially chitinized areas of the gizzard lining, whether they bear teeth or not. They may stand as abbreviations of "field" ("Felder" of Ris) or "fold." When the fields are approximately alike only one size letter may be used—F; when unlike, F will denote the largest sized areas, F medium sized, f small sized When the areas are of but two sizes F and f may be used.

Arabic figures following F, F, f, denote the number of teeth borne by each field respectively; when the number is great (40 or more) *n* is used to denote this fact. When in one and the same gizzard the teeth are of different sizes this is indicated by use of the marks ′, ″, ‴; ′ denotes the largest sized teeth, ″ medium sized, ‴ smallest sized.

Wherever a gizzard consists of a repetition of similar fields, the formula may be shortened by enclosing the repeated arrangement within parentheses, and placing the proper coëfficient before the parenthesis to indicate the number of times the repetition occurs.

When the same field contains two groups of teeth separated by a distinct interval, these two groups are indicated in the formula by placing one above the other with a horizontal line between them, as in common fractions, the anterior group of teeth being represented by the numerator, the posterior group of teeth by the denominator.

The abbreviation *rec.* is used to indicate recurved teeth, as in *Paraphlebia.*

To illustrate the application of the formula, I may refer to fig. 13, Pl. III, of *Argia bipunctulata.* In this species there are sixteen folds, eight larger and eight smaller. The formula would be therefore: 8 (F 12–14, f 1–3), where F represents the larger fields, with teeth varying in number from twelve to fourteen; f, the smaller folds with teeth varying from one to three.

The teeth here are all of approximately the same size.

For *Xanthagrion erythroneurum* (fig. 15), where the teeth have a definite arrangement into groups, we must use a more complicated formula. Here there are sixteen fields, each field showing two distinct groups of teeth. The anterior groups are represented by the numerators of the fractions, the posterior by the denominators. The difference in size of the teeth is indicated by the marks ′ and ″, the former representing the larger teeth, the latter the smaller ones.

The formula therefore is 8 $\left(F\,\frac{6''\text{-}8''}{2' - 10''\text{-}12''},\ f\,\frac{1''\text{-}3''}{5''}\right)$.

The omission of one or more folds from an individual gizzard is not uncommon (see fig. 12), so that often it is only possible to construct a formula when several specimens of a given species are examined and compared.

The following list of the species of adults whose gizzard-armatures have been studied gives the number of each sex examined, the abdominal segment in which the gizzard was found (and often whether in the anterior or posterior part of the segment), the locality whence the material came and the armature formula:

Sub-family CALOPTERYGINÆ.

Legion 1.—Calopteryx Selys.

Calopteryx maculata Beauv. 2 ♂. Pennsylvania. 4 (F 6–8, f 2–4, F 4–5, f 2–4).

Calopteryx apicalis Burm. ♂. 6th segment, ant. Tom's River, N. J. 4 (F 6–8, f 2–4, F 5–7, f 2–4).

Calopteryx apicalis Burm. ♀. 5th segment, ant. Tom's River, N. J. 4 (F 6–8, f 2–4, F 5–7, f 2–4).

Calopteryx cornelia Selys. 2 ♂. 5th segment, post. Japan. 4 (F 12–13, f 6–7, F 11–12, f 6–7).

Sapho orichalcea McLach. 1 ♀. 4–5th segments. Kamerun, W. Africa. 4 (F 5–7, f 5–6, F 6–7, f 5–6).

Sapho ciliata Fabr. 1 ♂. 5th segment, post. Bismarckburg, W. Africa. 8 (F 8–9, f 3–6).

Umma (*Cleis*) *longistigma* Selys. 1 ♂. Kamerun, W. Africa. 8 (F 20–25, f 3–5).

Mnais strigata Selys. 1 ♀. 4th segment. Japan. 4 (F 8–10, f 7–9, F 8–9, f 7–9).

Phaon fuliginosus Selys. 1 ♀. 6th segment. Madagascar. 4 (F 4–8, f 3–4, F 4–5, f 3–4).

Phaon fuliginosus Selys. 1 ♂. 3d segment. Madagascar. 4 (F 4–8, f 3–4, F 4–5, f 3–4).

Phaon iridipennis Burm. 1 ♂. 6th segment, post. Be Kilus. 4 (F 4–6, f 2–3, F 5–6, f 2–3).

Vestalis luctuosa Burm. 1 ♂. 6th segment, ant. Java. 4 (F 25–30, f 20–25).

Vestalis luctuosa Burm. 1 ♀. 5th segment, post. Java. 4 (F 25–30, f 20–25).

Vestalis gracilis Ramb. 1 ♂ and 1 ♀. 6th segment. Palone, Burma. 4 (F 20–25, f 15).

Vestalis amœna Selys. ♂ and ♀. 6th segment. Deli, Sumatra. 4 (F 15–20, f 10–12).

Vestalis apicalis Selys. ♀. 6th segment, ant. Nilgiris. 4 (F 10–15, f 8–10).

Hetærina occisa Selys. ♂ and ♀. 6th segment. Mexico. 8 (F n).

Hetærina titia Drury. ♂ and ♀. 6th segment. Texas. 4 (F n, f n).

Hetærina cruentata Ramb. ♂. 6th segment. Mexico. 8 (F n).

Hetærina vulnerata Selys. ♀. Dublan, Mex. 4 (F n, f n, F n, f n).

Hetærina vulnerata Selys. ♂. 5th segment. Dublan, Mex. 8 (F n, f n).

Hetærina americana Fabr. 4–6th segments. Tepic, Mex. 4 (F n).

Hetærina americana. ♂. 6th segment. Pennsylvania. 4 (F n″ + 4′–6′, f n″ – 3′–6′).

Hetærina americana. Larval-gizzard from preceding ♂. 4 (F n″ + 8′–12′, f n″ – 5′–6′).

Legion 2.—**Euphæa** Selys.

Euphæa impar Selys. 1 ♂. 5th segment, post. Borneo. 8 (F n, f 0-n, F n, f 0-n). The fields, f, which are very short, vary greatly in the number of teeth; these in some cases being numerous, in others 2–4, in others seeming to be absent altogether.

Euphæa lara Krüger. 1 ♂. 6th segment, post. Borneo. 8 (F n, f 0-n, F n, f 0-n).

Euphæa variegata Ramb. ♂. Java. 8 (F n, f n, F n, f n).

Euphæa ochracea Selys. ♂. Sixth segment, post. Burma. 8 (F n, f n, F n, f n).

Epallage fatime Charp. ♀. 4th segment. Taurus, Asia Minor. 8 (F n, f n).

Legion 3.—**Amphipteryx** Selys.

Amphipteryx agrioides Selys. 2 ♂. 6th segment. Guatemala. 8 (F 8–10, f 4–5).

Legion 4.—**Libellago** Selys.

Libellago curta Selys. ♂. 4th segment. Abyssinia. 4 (F 10–14, f 6–8, F 10–12, f 6–8).

Libellago caligata Selys. ♂. 5th segment. Abyssinia. 4 (F 12–15, f 5–9, F 12–16, f 6–9).

Libellago caligata Selys. ♀. 3d segment. Abyssinia. 4 (F 12–15, f 5–9, F 12–16, f 6–9).

Rhinocypha biseriata Selys. ♀ and ♂. 4th segment. Borneo. 4 (F 6–9, f 3–5, F 6–8, f 3–5).

Rhinocypha Pagenstecheri Först. ♂. Sumbawa. 4 (F 8–10, f 5, F 7–10, f 5).

Micromerus lineatus Burm. 3 ♂. 5th segment. Java, Ceylon. 4 (F 10–13, f 3–5, F 9–10, f 3–5).

Micromerus obscurus Kirby. ♂. 5th segment. Ceylon. 4 (F 10, f 4–6, F 6–8, f 4–6).

Legion 5.—**Thore** Selys.

Thore boliviana McLach. ♂. 5th segment. Chulumani, Bolivia. 4 (F n, f n)?

Thore boliviana McLach. ♀. 7th segment, ant. Chulumani, Bolivia. 4 (F n, f n)?

Euthore hyalina Selys. ♀. 5th segment, post. Road to Coroico, Bolivia. 4 (F n, f n)?

Cora marina Selys. 2 ♂. 5th segment, post. Vera Cruz. 4 (F n, f n)?

Cora inca Selys. ♀. 6th segment. Chulumani. 4 (F n, f n)? These became so much broken in dissection and mounting that the formula cannot be stated positively. Some seem to show twelve bands.

Sub-family AGRIONINÆ.

Legion 1.—Pseudostigma Selys.

Megaloprepus cœrulatus Drury. 2 ♂. 6th segment. 8 (F 30–35, f 20–25).

Microstigma rotundatum Selys. 1 ♂. 7th segment, ant. Bolivia. 4 (F 35–40, f 10–16, F 30–35, f 10–16).

Microstigma anomalum Ramb. ♂. 6th segment. Apehu, Brazil. 4 (F 18–20, f 6–8, F 10–12, f 6–8).

Anomisma abnorme McLach. 6th segment. Rio Bobonaza, Ecuador. 8 (F 18–20, f 8–10)?

Mecistogaster modestus Selys. ♀. Bugaba. 8 (F n, f n).

Mecistogaster ornatus Ramb. ♂. 7th segment. Tepic, Mex. 8 (F n, f n).

Pseudostigma aberrans Selys. ♂. 5th segment. Atoyac, Mexico. 8 (F n, f n)?

Legion 2.—Podagrion Selys.

Paraphlebia sp. (group of *Zoe*). 5 ♂, 1 ♀. 6th segment. Guatemala. 8 (F 2′ + 11″–13″ + 4″–5″ rec., f 3″–4″).

Paraphlebia sp. (group of *Zoe*) var. ♂. Misantla, Mexico. 8 (F 2′ + 8″–9″ + 2″ rec.).

Philogenia Berenice Hag. ♂. 6th segment. Equitos, Peru. 8 (F n, f n).

Philogenia cassandra Hag. ♂. 6th segment. Chiriqui. 8 (F n, f n). Teeth much smaller than in *Berenice*.

Megapodagrion venale Selys. ♂. 6th segment. Probably Porto Cabello, Venezuela. 8 (F 3–7, f 1–2).

Heteragrion erythrogastrum Selys. ♂. 7th segment. Bugaba. 4 (F n, f n).

Heteragrion chrysops Hag. ♂. 6th segment, post. Guatemala. 4 (F n, f 5–8, F 30–35, f 5–8).

Heteragrion chrysops Hag. ♂. 7th segment, ant. Guatemala. 4 (F n, f 5–8, F 30–35, f 5–8).

Heteragrion inca Hag. 2 ♂. 5–6th segment, 7th segment, ant. 4 (F n, f 20–25, F n, f 20–25).

Heteragrion n. sp. (group of *Chrysops*). ♂. Atoyac, Mexico. 8 (F n, f 5–35).

Legion 3.—**Platycnemis** Selys.

Tatocnemis malagassica Kirby. ♀. 7th segment. Madagascar. 8 (F $\frac{n'}{n''\ \text{rec.}}$, f $\frac{20'–30'}{0}$).

Leptocnemis bilineata Selys. ♂. Seychelle Islands. 8 (F n, f 15–20).

Leptocnemis bilineata Selys. ♀. Seychelle Islands. 4 (F n, f 12–19, F n, f 12–19).

Cœliccia octogesima Selys. ♂ and ♀. 7th segment, ant. Borneo. 4 (F 6–12, f 2–4, F 5–8, f 2–4).

Copera atomaria Selys. ♂. 6th segment, post. Borneo. 4 (F 5′–7′ + n‴ rec., f 1″–2″, F 4″, f 1″–2″).

Legion 4.—**Protoneura** Selys.

Disparoneura analis Selys. ♂. 6th segment, post. Borneo. 4 (F 3′ + n″, f 3′ + n″).

Disparoneura collaris Selys. ♂ and ♀. 6th segment, post. Borneo. 4 (F n, f n).

Disparoneura sp. (near *delia*). ♂. Borneo. 4 (F n, f n)?

Caconeura dorsalis. ♂ and ♀. 7th segment, ant. Borneo. 4 (F n, f n).

Neoneura n. sp. (group of *carnatica*). ♂. 7th segment, ant. Guatemala. 4 (F 2′ + 2″–4″, f 1′, F 2′ + 1″–2″, f 1′).

Neoneura n. sp. (group of *rubriventris*). ♂. 7th segment, ant. Equitos, Peru. 8 (F 2′ + 20″–30″, f 1′–2′ + 10″–20″).

Protoneura n. sp. (group of *humeralis*). ♂. 6th segment, post. Guatemala. 8 (F 2′ + n″, f 1′ + n″).

Protoneura aurantiaca Selys. ♂. 7th segment, ant. Tabasco, Mex. 8 (F 1′–2′ + n″, f 1′ + n″).

Protoneura n. sp. (group of *sancta*). 2 ♂ and 2 ♀. 7th segment, ant. Tabasco, Mex. { 8 (F 2′ + n″, f 1″ + n″).
{ 8 (F 2′ + n″, f n″).

Legion 5.—**Agrion** Selys.

Hyponeura lugens Hag. ♂. 6th segment. Guatemala. 8 (F 17–25, f 4–7).

Hyponeura lugens Hag. ♂. 5th segment, post. Guatemala. 8 (F 17–25, f 4–7).

Argia putrida Hag. ♂. 5th segment. 8 (F 14–21, f 2–10).

Argia bipunctulata Hag. New Jersey. 8 (F 12–14, f 1–3).

Argia agrioides Calv. ♂ and ♀. San Jose del Cabo, Baja Cal. 4(F $\frac{10'\ 14'}{10''–14''\text{ rec.}}$, f 2′–5′, F 11′–15′, f 2′–5′).

Argia pulla Selys. ♂. Tepic, Mex. 8 (F 7–9, f 2–3).

Ischnura heterosticta Burm. ♂. 6th segment. Victoria, Australia. 8 (F 13–15).

Ischnura Ramburii Selys var. *credula*. ♀. San Jose del Cabo. 8 (F 10–15).

Anomalagrion hastatum Say. ♂. Pennsylvania. 8 (F 9–10).

Enallagma ebrium Hag. ♀. 6th segment. New York. ? 8 (F 16′–18′ + 6″–12″, f 0–3′ + n″).

Enallagma geminatum Kell. ♀. 6th segment. New York. 4 (F 15′–18′, f n″, F 14′–16′, f n″).

Enallagma aspersum Hag. ♂. 6th segment. New York. 8 (F 20′–22′, f n″).

Nehalennia lais Brauer. ♂. 6th segment. Morelos, Mex. 4 (F 25–30, f 18–20).

Pyrrhosoma tenellum Vill. ♂. 5th segment. Le Blanc, France. 8 (F 25–30, f 8–12).

Pyrrhosoma minium Harr. ♂. Le Blanc, France. 8 (F 2′ + n″).

Xanthagrion erythroneurum Selys. ♂. Victoria, Australia. 8 (F $\frac{6''–9''}{2' + 10''–13''}$, f $\frac{1''–3''}{5''}$).[6]

Ceriagrion glabrum Burm. 3 ♂. 6th segment, post. Madagascar. 8 (F 2′ + 18″–20″, f 5″–10″).

Anisagrion allopterum Selys. ♂. 6th segment. Costa Rica. 8 (F 10–12, f 1–2).

Erythagrion salvum Hag. ♂. San Jose del Cabo, Baja Cal. 8 (F 2′ + 4″–6″, f 1″).

Erythagrion salvum Hag. ♂. San Jose del Cabo, Baja Cal. 8 (F 7–9, f 1–2).

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[6] It is quite likely that this is a larval gizzard; compare with figs. 25–27.

Leptagrion macrurum Burm. ♂. 7th segment, ant. Brazil. 8 (F 6′–8′ + n″, f 10″–20″ + 2′–3′).

Leptobasis vacillans Selys. 2 ♂. 7th segment, ant. Tabasco, Mex. 4 (F 13–15, f 10–12).

Agriocnemis femina Brauer. ♂. 6th segment. Borneo. 4 (F 10–15, f 8–10)?

Hemiphlebia mirabilis Selys. ♀. Victoria. 4 (F 2′–4′ + n″, f n″, F n″, f n″).

Legion 6.—**Lestes** Selys.

Archilestes grandis Ramb. ♂. San Jose del Cabo, Baja Cal. 8 (F n).

Lestes disjunctus Selys. 6th segment, New York. 8 (F n).

Lestes vigilax Selys. ♂. New York. 4 (F n, f n).

Lestes leda Selys. ♂. 6th segment. Victoria. 4 (F n, f n).

Lestes tenuatus Ramb. ♀. Tepic, Mex. 8 (F n)?

Intra-generic Variations.

By an examination of the structural formulæ given above it will be seen that a classification into genera based on resemblances in gizzard structure would agree in most cases with that now in use based upon the structure of wings and other external features of the body. If, for instance, we examine the structural formulæ for *Sapho orichalcea* and *S. ciliata*, we find very little difference between the two species. In both we see sixteen fields, which in the former are of three sizes, and in the latter of two. But the number and size of the teeth are approximately equal.

Where a number of species of one genus have been studied, these all, as a rule, show the same number of folds. Exceptions are seen in the genera *Hetærina* and *Heteragrion*. Of five species of *Hetærina* examined, four show eight folds of the gizzard lining, and one, *americana*, four folds, although another specimen of the same species (Pl. II, figs. 2 and 3) shows eight folds in both larval and adult gizzard linings; of four species of *Heteragrion* three have sixteen folds; one, eight.

Even when they vary in the number of folds, species of the same genus are seen to agree almost invariably in the size and number of teeth on each fold, as well as in the arrangement of these.

A marked exception to this was found in the genus *Heteragrion*. Of four species of this genus, three had sixteen folds, varying in size, the largest folds bearing numerous teeth (above forty), the smaller ones bearing from five to thirty, while the fourth species had but eight folds, each fold bearing numerous teeth.

Again, of four species of *Argia*, three are similar, bearing eight "F" folds and eight "f" folds, the teeth on all folds being of equal size. But in the fourth species, *A. agrioides*, there are four "F" folds, eight "f" folds, and four "F" folds; on the two latter the teeth are equal in size, but on the four "F" folds they are arranged in two groups, those of the anterior group being similar to the teeth on the other folds, those of the posterior being much smaller and recurved.

Data for Phylogeny.

When the studies whose results are contained in the present paper were begun, it was hoped that they would yield data of value in determining the phylogeny of the insects investigated. The data are now at hand, but the desired interpretation is yet to be made. One may spin several different theories on the lines of descent of these *Odonata* if regard be had merely to the armature of the gizzard. But since these theories would rest on precisely the same evidence in each case, it is wise to refrain from such theorizing until these results can be correlated with others drawn from embryological and comparative anatomical data.

It is worth pointing out, however, as one present gain to our knowledge which will bear on the question of phylogenies, that the occurrence of numerous minute teeth only is a phenomenon of frequent repetition, since it is met with in the genus *Hetærina* of the legion *Calopteryx*, and in all species of the legions *Euphæa* and *Thore* of the *Calopteryginæ*, while in the *Agrioninæ* it is observed in *Mecistogaster* and *Pseudostigma* (legion *Pseudostigma*), *Philogenia* (legion *Podagrion*), some *Disparoneura* and *Caconeura* (legion *Protoneura*) and all of the legion *Lestes*.

The problem which this phenomenon suggests is to determine whether it represents a more primitive condition, originally common to all groups to which the genera named belong, or whether it represents independent, parallel and similar modifications in each group from some other and different form of gizzard-armature.

EXPLANATION OF PLATES II, III AND IV.

All the figures are camera lucida drawings, and represent portions of the gizzard linings, spread out flat. The fraction after each name indicates how much of each lining is shown. A line indicting a scale length of one-tenth millimeter is placed alongside most of the figures.

Plate II.

Fig. 1. *Calopteryx maculata.* ♂. $\frac{1}{4}$.
Fig. 2. *Hetærina americana.* ♂ from Pennsylvania. $\frac{1}{4}$.
Fig. 3. *Hetærina americana.* Larva. $\frac{1}{4}$.
Fig. 4. *Protoneura* sp., group of *sancta.* ♀. $\frac{1}{8}$.
Fig. 5. *Hetærina vulnerata.* ♀. $\frac{1}{4}$.
Fig. 6. *Vestalis luctuosa.* ♂. $\frac{1}{4}$.
Fig. 7. *Vestalis apicalis.* ♀. $\frac{1}{4}$.
Fig. 8. *Amphipteryx agrioides.* ♂. $\frac{1}{8}$.
Fig. 9. *Libellago caligata.* ♂. $\frac{1}{4}$.
Fig. 10. *Euphæa impar.* ♂. $\frac{1}{4}$.

Plate III.

Fig. 11. *Microstigma rotundatum.* ♂. $\frac{1}{4}$.
Fig. 12. *Enallagma ebrium.* ♀. $\frac{3}{16}$. The small fold f is not developed in the portion figured.
Fig. 13. *Argia bipunctulata.* $\frac{1}{8}$.
Fig. 14. *Megaloprepus cœrulatus.* ♂. $\frac{1}{8}$.
Fig. 15. *Xanthagrion erythroneurum.* $\frac{3}{16}$. Probably larval gizzard; compare figs. 25–27.
Fig. 16. *Megapodagrion venale.* ♂. $\frac{1}{8}$.
Fig. 17. *Ischnura verticalis.* $\frac{1}{4}$.
Fig. 18. *Heteragrion inca.* ♂. $\frac{1}{4}$.
Fig. 19. *Tatocnemis malagassica.* ♀. $\frac{1}{8}$.
Fig. 20. *Paraphlebia* sp. $\frac{1}{8}$.
Fig. 21. *Hemiphlebia mirabilis.* ♀. $\frac{1}{8}$.
Fig. 22. *Lestes vigilax.* ♂. $\frac{1}{4}$.
Fig. 23. *Mnais strigata.* ♀. $\frac{1}{4}$. On either side of the right-hand f fold is a row of 2–3 teeth, representing, probably, a series of still smaller folds.
Fig. 24. *Leptocnemis bilineata.* ♂. $\frac{1}{8}$.

Plate IV.

Fig. 25. *Ischnura verticalis.* Larva, length 4 mm. $\frac{15}{16}$.
Fig. 26. *Ischnura verticalis.* Larva, length 8 mm. $\frac{1}{2}$.
Fig. 27. *Ischnura verticalis.* Larva, length 15 mm. $\frac{1}{2}$.